Differential spatial representation of precision and power grasps in the human motor system

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ABSTRACT

Power and precision grasps are two interrelated, kinematically distinct types of finger movements. We examined whether these types of motor actions may be spatially differently represented in the human central nervous system.

In healthy participants representations of finger movements were mapped by delivering single pulse TMS to multiple scalp regions covering the left primary motor cortex (M1). Finger joint motions were recorded from the right hand using a data glove. Principal component analysis was used to extract local subspaces representing the TMS-evoked movement data from each scalp region. Voluntary power and precision grasps were reconstructed with these subspaces. The spatial properties of these reconstructions were analyzed for each grasp type using a general linear model.

We found overlapping, yet distinct spatial representations for precision and power grasps with precision grasps represented slightly posterior compared to a more uniform distribution for power grasps. Differential spatial encoding of both grasp types may point towards a representation of power grasps within a phylogenetically older M1 area at the crown of the precentral gyrus and of precision grasps in a newer area in the depth of the central sulcus. Results also support the idea of separate synergistic movement representations in the human motor system.

1. Introduction

Human finger movements display a high degree of complexity during grasping and manipulation of objects. Traditionally, human grasp patterns have been dichotomized (Napier, 1956) with power grasps referring to the action of holding an object with the long fingers forcefully curled around it and precision grasps allowing for a delicate manipulation of objects. While grasps involving all fingers can be found in many tetrapodes (Sustaita et al., 2013), precision grasps require individuation of finger movements which only are fully developed in humans along with the emergence of precise tool usage (Marzke, 1983; Antinucci and Visalberghi, 1986; Marzke, 1997; Almécija et al., 2010). This phylogenetic sequence seems to be reflected in ontogenesis: Grasp reflexes consisting of flexion movements of all fingers are the first finger movements observed in human newborns. These reflexes are later replaced by voluntary power grasps, and finally complemented by individual finger movements during precision grasps (Halverson, 1931; Butterworth et al., 1997). What may appear as an evolutionary argument for a differential

encoding of particular grasp patterns, may be supplemented by neuro-anatomical evidence. The primary motor cortex harbours two cytoarchitectonically separable motor regions (Geyer et al., 1996; Rathelot and Strick, 2006, 2009; Dea et al., 2016), which have been discussed as possible substrates for independent finger movements and whole-hand grasps (Maier et al., 1993; Rathelot and Strick, 2006, 2009).

A fundamental problem in motor control is the fact that movements may be generated out of a very large set of possible combinations of muscle activations and joint postures. This problem, also known as the degrees-of-freedom problem (Bernštejn, 1967), may be particularly pertinent for grasping movements because of their remarkable flexibility and variability. The idea that a large variety of diverse movements can be generated out of recombinations of small sets of elementary covariant neuronal activation patterns, also termed "synergies", has been offered as a possible solution (Bernštejn, 1967; Bizzi et al., 1991; Tresch et al., 2002). Synergies have been inferred from electromyographic recordings as well as from kinematic data by applying mathematical factorization techniques (d'Avella and Tresch, 2002; d'Avella et al., 2003; Tresch,

2006; Torres-Oviedo and Ting, 2007). However, a number of authors have pointed out that synergies may also arise when voluntary movements are studied in experimental settings because the space of performed movements is limited by experimental design rather than limited movement capabilities (Kutch et al., 2008; Tresch and Jarc, 2009; Kutch et al., 2012). These so-called task constraints may be minimized by analyzing involuntary movements generated from "reading out" the resting motor cortex using brain stimulation. This approach may allow to uncover synergistic patterns as a principle of neuronal organization (Schieber and Santello, 2004; Tresch and Jarc, 2009; Groote et al., 2014; Steele et al., 2015).

The analysis of neuronal activation patterns recorded from M1 has not revealed a separation of precision and power grasping movements; rather, there was substantial spatial electrophysiological overlap in sensorimotor areas including M1 (Spinks et al., 2008; Townsend et al., 2011; Raffin et al., 2015). In non-human primates electrical muscular activity evoked by direct electrical cortical stimulation has been shown to be closely related to natural movements structured into synergies (Overduin et al., 2012, 2014). Even though representations of hand and arm movements displayed a distinct cortical organization at the level of the primary motor cortex (Graziano et al., 2002; Graziano, 2005; Overduin et al., 2012, 2014), distinct classes of grasping movements were not associated with particular cortical sites in these studies. In humans, differential blood oxygen level dependent (BOLD) responses in premotor areas and near M1 pointed to a dissimilar representation of precision and power grasps in grasping tasks in one study (Ehrsson et al., 2000), but not in another (Kuhtz-Buschbeck et al., 2008). Additionally, a recent neuroimaging study showed evidence in favor of the neuronal basis of synergistic finger movements (Leo et al., 2016). A study employing transcranial magnetic stimulation (TMS) demonstrated that M1 activity related to grasps which were about to be performed by the subjects may be differently primed by viewing images of objects with different power or precision grasp affordances (Bartoli et al., 2014). Although these studies hinted at anatomical separations of motor representations, separation of precision and power grasps at the level of the primary motor cortex and its efferent projections was not described.

In the present study, we combined the analysis of finger movements evoked by brain stimulation with the recordings of voluntary precision and power grasps to obtain additional insight into the organization of these types of movements in humans. We employed a TMS mapping procedure, as, for ethical reasons, invasive studies addressing the representation of grasping cannot be done in healthy humans. Building on techniques established previously (Gentner and Classen, 2006; Gentner et al., 2010), we aimed to investigate whether precision and power grasps are spatially differently represented in the human motor cortex and whether this distribution would be compatible with the hypothesis that precision grasps may be encoded in the phylogenetically newer posterior part of the primary motor cortex within the central sulcus, while power grasps may be represented more anteriorly.

2. Material and methods

2.1. Experimental procedures

The study conformed to the principles of the declaration of Helsinki and was approved by the local ethics committee at the University of Leipzig. Eighteen right-handed and neurologically healthy human subjects (12 male, 6 female) participated in the experiment. Right-handedness was confirmed using the Edinburgh Handedness Inventory (Oldfield, 1971); we did not include professional musicians. Informed written consent was obtained from all participants.

Participants received suprathreshold TMS over and surrounding the left primary motor cortex with the goal to evoke synergistic finger movements that were recorded using a data glove. Afterwards, they performed grasps for real objects. The relationships between TMS-evoked joint excursions and grasp kinematics were analysed with

respect to the type of grasping movements performed (precision or power grasp).

Three participants were excluded from the study or the analysis: One subject (male) fainted during the TMS procedure before data acquisition was completed. In two subjects (1 male, 1 female) no or only very slight movements were obtained during the TMS mapping procedure, presumably because their stimulation thresholds had been determined erroneously low. These datasets were too small for further analysis. Therefore, data from 15 subjects (10 male, 5 female, age 25.8 ± 2.5 years) were used in the analysis.

Transcranial magnetic stimulation mapping procedure. We aimed to evoke finger movements by stimulating different parts of the primary motor cortex (M1) with suprathreshold TMS. First, the resting motor threshold (RMT) of the right abductor pollicis brevis muscle (APB) was determined using suprathreshold single pulse TMS (MagStim 200, 70 mm figure-of-eight coil, MagStim Company Ltd., Whitland, UK) and surface EMG recordings (Digitimer D360, Digitimer Ltd., Hertfordshire, UK). Multiple TMS single pulses were applied at stimulation sites overlying the left motor region with the coil oriented at 45 deg against the sagittal and frontal planes of the subject. The site yielding the largest MEP amplitudes was determined as the APB hot spot. The RMT was then determined stimulating at the hot spot using an adaptive parameter estimation by a sequential testing algorithm implemented in a freeware software tool ("Adaptive PEST for TMS", *www.clinicalresearcher.org/software.htm*). Mean RMT across all 15 subjects was 48.3% ±9.8% of maximum stimulator output.

High resolution structural MRI datasets were obtained at 3 T on a Siemens Verio (Siemens Healthcare, Erlangen, Germany) MR system using a MP-RAGE sequence (Mugler and Brookeman, 1990) with a voxel size of either $1 \times 1 \times 1$ mm or $1 \times 1 \times 1.5$ mm. APB hot spot location and stimulation sites were co-registered with the structural MRI scan using a BrainSight 2 neuronavigation system (Rogue Research Inc., Montreal, Canada). As targets for TMS, we predefined 49 stimulation sites overlying the motor cortex using a virtual map of 7×7 points (horizontal and vertical spacing 8 mm) which was created in the BrainSight 2 software around each individual APB hot spot. The grid was aligned approximately parallel to the sagittal and frontal planes. Then the grid location was tested using suprathreshold TMS pulses which were applied at 140% RMT over scalp sites at the borders of the virtual map. At this stimulation intensity corticospinal projection neurons are activated predominantly indirectly. When TMS evoked movements on locations outside of the map, the map was moved to include these stimulation sites. If the map was too small to encompass all sites where movements could be evoked by TMS, the stimulation intensity was reduced to 130% RMT prior to the start of the mapping procedure after which intensity was kept constant. Mean stimulation intensity used was 136.6% RMT.

Afterwards, for the actual TMS mapping procedure, we randomly navigated to each of the 49 sites on the digital map and applied 15 single magnetic pulses (in total 735) at a frequency of 0.25 Hz. A custom built data glove (Gentner and Classen, 2009) with bend sensors over metacarpophalangeal (MCP) and proximal interphalangeal (PIP) joint of every finger (in total 10 sensors) of the right hand was used to record finger twitches evoked by TMS (Fig. 1A). During this procedure, the right hand was kept in a semipronated position as the distal forearm was placed in a mould, supported by a cushion. This enabled a relaxed position and the recording of unconstrained finger movements minimizing gravitational bias. Data were sampled at 150 Hz with custom made software written in C++ (Microsoft Visual Studio 2009, Microsoft Corp., Redmond, USA) and Java (Oracle, Redwood Shores, USA). Data sampling was started 0.5 s before the software triggered a TMS pulse and continued for a total of 2 s for every pulse always encompassing the evoked twitches.

Natural grasping movements. Following the mapping procedure, participants were asked to perform the Jebsen-Taylor Test of Hand Function wearing the data glove (JHFT, Jebsen et al., 1969). This test contains a number of tasks involving grasps for real physical objects ("picking up small objects", "stacking of checkers", "lifting light cans" and "lifting